

# LEAVES OF THE FARINOSAE<sup>1</sup>

AGNES ARBER

(WITH PLATES I-III)

## Introduction

In papers published in this and other journals during the last few years (ARBER 1-10) I have dealt with the results of the application of the phyllode theory to the leaves of various groups of monocotyledons. The present paper discusses, from this standpoint, the leaf structure of the families associated by ENGLER (11) in the cohort Farinosae. Examination of this group is a matter of some difficulty to a British botanist, since the eleven families which it includes are represented in Europe by one species alone, *Eriocaulon septangulare* With., and even in cultivation comparatively few genera belonging to these families are to be found. I have thus been unable to carry this study so far as I should have wished, because it has been necessary to rely almost entirely on limited quantities of herbarium material, which, in the case of the many fibrous-leaved members of the Farinosae, is peculiarly intractable to sectioning. MCLEAN'S (14) method of preparing dried material has proved invaluable, however, even in the case of plants which have lain in herbaria for many years. The specimen of *Cephalostemon affinis* Koern., for instance, sections of which are represented in fig. 26 A-C, was collected by SPRUCE in South America as long ago as 1853.

I am indebted for material to the Director of the Royal Botanic Gardens, Kew; the Keeper of the Department of Botany, British Museum (Natural History); Mr. L. RODWAY, of Hobart, Tasmania; and Professor A. C. SEWARD.

I propose in the first place, taking the families in the order in which they appear in ENGLER'S *Pflanzenfamilien*, briefly to describe the principal types of leaf met with in the cohort, and then to discuss their interpretation.

<sup>1</sup>This paper represents part of the work carried out during the tenure of a Keddey Fletcher-Warr Studentship of the University of London.



### Flagellariaceae

I hope to describe the leaves of this family in a later paper, so I will omit all discussion of them here; their most unusual feature is that, in the genus *Flagellaria*, they have tendril apices.

### Restionaceae

In this family, which consists of nineteen genera, plants with radical leaves are rare. The genus *Anarthria*, however, forms a notable exception, for it has basal leaves recalling those of *Iris*, which may either be ensiform or "radial." Fig. 3 *A* represents the transverse section of the limb of *Anarthria scabra* R.Br. It will be seen that it has a type of anatomy resembling that of an *Acacia* phyllode, the bundles, which are in two series lying to right and left of the median plane of the leaf, having their xylems directed inward. The palisade parenchyma is interrupted at very short intervals by bands of fibers, one of which occurs between each of the main bundles and the epidermis, while others are associated with the smaller bundles, or occur independently. Fig. 3 *B* shows the margin of such a leaf, with the median bundle, on a larger scale. Two of the fibrous bands (*f*) are visible, and it will be seen that, in the marginal region, the palisade parenchyma passes over into thick-walled elements without contents. The epidermal cells also increase in size and in the thickness of their sclerised walls as the margin is approached. Fig. 4 *A-C* shows the leaf of *Anarthria gracilis* R.Br., which, instead of being ensiform like that of *A. scabra*, is radial. The limb (*C*), in which the fibrous sheaths of the bundles with their extensions to the epidermis form a conspicuous feature, is almost cylindrical in section. The leaves of *Anarthria*, however, are not typical for this family, in which it is usual to find cauline leaves alone. Such leaves generally have a well developed sheath, succeeded by a relatively unimportant limb, which may be flattened or cylindrical, but is often reduced to a mere point (examples occur in *Dovea*, *Elegia*, *Lepyrodia*, and a number of other genera). Fig. 1 *A* shows the appearance of the leaf of *Restio tremulus* R.Br. It has a sheathing base (*s*) which more than surrounds the axis, forming a "wrap-over." The same peculiarity in other members of this family may be carried to a further point; in a species of



*Thamnochortus*, the sheathing base of the scale leaf is described by VELENOVSKÝ (18) as surrounding the axis spirally, and, according to his fig. 358, its attachment forms more than two complete turns round the axis. Both sheath and narrow, flat limb of *Restio tremulus* are fibrous (fig. 1 B, C), and toward the apex of the limb there is a marked increase in the lignified and sclerised tissue (fig. 1 D). The leaf of *Leptocarpus peronatus* Mast., with its sheathing base and limb reduced to a mucro, is represented in fig. 2. In the case of *Elegia deusta* Kth. the leaf apex is more solid, and includes a ring of bundles (10, fig. 5 A, B).

### Centrolepidaceae

The leaves of the Centrolepidaceae are usually small, with a sheathing base and an awl-like or threadlike limb. *Gaimardia australis* Gaudich. (fig. 5 A-C) may be taken as an example. There is a sheathing leaf base and an awl-like limb, traversed by three bundles inclosed in fibrous sheaths. The leaves of this family may be of a more reduced type, however, as in *Centrolepis aristata* R. and S. In this plant I have found one bundle, traversing both sheath and limb (fig. 11 B, C). GOEBEL (13), on the other hand, describes and figures the leaf anatomy of this species as belonging to an extremely reduced ensiform type, with a second bundle above the median bundle, resulting from the fusion of two laterals. Although I have not found this structure in the only two foliage leaves which I was able to examine, I have seen it in two of the bracts from the base of the inflorescence (b, fig. 11 A). These bracts are well developed structures with a sheath and limb, closely resembling the foliage leaves.

### Mayacaceae

The very delicate leaves of the single aquatic genus *Mayaca*, of which this family consists, are traversed by a single vascular strand (fig. 27 A). Several species figured in the *Flora Brasiliensis* (17) have a bifid leaf apex, such as is shown here for *M. fluviatilis* Aublet (fig. 27 B). It will be seen that the vascular bundle (vb) takes no part in the bifurcation, but terminates below the fork.



### Xyridaceae

This family consists of two genera, *Xyris* and *Abolboda*. *Xyris*, which includes about forty species, has a leaf with a sheathing base and an ensiform limb, recalling that of many members of the genus *Iris*. In *Xyris Wallichii* Kth. (figs. 12 A-C) and *X. brevifolia* Mich. (fig. 18 A, B) the single bundles alternate to right and left in the flattened limb. Fig. 18 B shows the marginal strand of *Xyris brevifolia*, which is peculiar in the possession of a conspicuous mass of fibers adjoining the bundle on the xylem side, whereas such a fibrous strand is more usually developed outside the phloem. As POULSEN (16) has already shown, the vascular bundles of the leaves of *Xyris* may either be single or associated in groups of two or more. Figs. 13 and 14 show bundle groups in the case of *X. asperata* Kth. (*trachyphylla* Mart.) and *X. anceps* Lam. These bundle groups may attain considerable complexity; that represented in fig. 13 B (*X. asperata*) consists of nine strands imbedded in a common fibrous sheath. Although the flattened ensiform leaf type is usual in *Xyris*, it is not universal. POULSEN (16) has figured a species (*X. teretifolia* Poulsen) in which the transverse section of the leaf limb is oval, the distance between the adaxial and abaxial margins being only about half as much again as the width.

In *Xyris* the leaf epidermis is generally thick-walled. It may retain much the same character at the two margins as on the flanks of the leaf (*X. Wallichii*, fig. 12 C), or the elements at the margins may be considerably elongated, forming a fibrous border to the leaf (*X. anceps*, fig. 14 B-D). In this case the marginal elements, instead of standing out horizontally, slope downward, with the result that they are cut obliquely in transverse sections passing through the leaf border, which at first glance thus suggest that the epidermis is multi-layered in this region (fig. 14 D).

*Xyris gracilis* R.Br. is significant as possessing sheathing leaves, in which the limb may be reduced to a mere point, and in which the leaf base forms practically the whole organ (fig. 17). These leaves may be compared with those of the second genus of Xyridaceae, *Abolboda*. I have examined the leaves of *A. grandis*



Griseb. var. *minor*, and find them to be traversed by a single series of normally orientated bundles, corresponding to those in the sheath leaves of *Xyris gracilis* (fig. 17 C). *A. Poarchon*, as figured by SEUBERT (17), has an acuminate apex to the foliage leaf, while it also has bracts which terminate in a "cornet," recalling that described by HALLIER in the case of the sepals of certain dicotyledons (see reference and discussion, 10). It is probable that the apex in both foliage leaf and bract of *A. Poarchon* Seub. is a vestigial petiole, and is morphologically equivalent to the ensiform limb of *Xyris*.

### Eriocaulaceae

The Eriocaulaceae have both cauline and radical leaves of a simple type. The two principal genera are *Eriocaulon* and *Paepalanthus*, both of which include more than a hundred species. Fig. 19 A shows the general internal structure of the British species of *Eriocaulon*, *E. septangulare* With. A large proportion of the leaf is occupied by lacunae, separated by lamellae, each of which includes a single normally orientated bundle. Fig. 19 B shows one lamella with its vascular strand on a larger scale. A fragment of a diaphragm (*d*) with intercellular spaces between its cells is seen attached to the lamella on one side. In *E. cuspidatum* Dalz. the limb terminates in a mucro (fig. 19 D), while in *E. Wallichianum* Mart. f. *submersa* the tip of the ribbon leaf is minutely truncate (fig. 19 C). In this aquatic species, as in so many water plants, there is an increase of the tracheal tissue near the leaf apex, and there are indications of water stomates and possibly an apical opening, but in herbarium material it is difficult to identify these structures with certainty. The leaves of certain species of *Eriocaulon* may be much reduced; in the aquatic *E. setaceum* L. the fragile linear leaf, traversed by a single bundle, recalls that of *Mayaca*. In the case of *Paepalanthus* I have examined one species, *P. speciosus* Gardn. Here, as in *Eriocaulon*, there is one series of normally orientated bundles in the leaf. The large epidermal cells are a striking character.

### Rapateaceae

The leaves of this family are much larger and more complex than those of the Eriocaulaceae; they may show a definite differ-



entiation into sheath, petiole, and limb (*Rapatea longipes*, fig. 24). A curious feature common to the leaves of various members of the family is their tendency to asymmetry. The leaf sheath, as ENGLER points out in the *Pflanzenfamilien*, is folded, but the median bundle does not occupy the trough of the fold, and the limb correspondingly is not of equal width on either side of the midrib. These features are shown in fig. 24, *Rapatea longipes* Spr.; fig. 25 A, B, *R. angustifolia* Spr.; and fig. 26 A, B, *Cephalostemon affinis* Koern. In the last species the sheath is peculiar, since it thins out markedly at the fold, which is quite remote from the median bundle, whose position is marked externally by a ridge of fibrous tissue (*f*) adjacent to the lower surface (fig. 26 A). This ridge can also be recognized in the limb (fig. 26 B). The lacunate character of the leaf tissue in *Rapatea angustifolia* Spr. is indicated in fig. 25 C, which also shows the median bundle with its fibrous sheath, and the small fibrous strands which run beneath the epidermis. The details of the median bundle of the limb of *Cephalostemon affinis* are seen in fig. 26 C.

### Bromeliaceae

The leaves of the Bromeliads are often of a simple type, with a broadly sheathing base prolonged into a linear to ovate limb. In some cases, however (*Tillandsia usneoides* L. fig. 20 A, B), there is a marked distinction between the sheathing leaf base and the limb, which has a definitely petiolar character. In other cases the main part of the leaf suggests a leaf base, but there is a solid apical region which may correspond to the limb of *Tillandsia usneoides* on a reduced scale (10). The figures of *Aechmea gamosepala* Wittm. in the *Flora Brasiliensis* (15) show that the foliage leaves in this case have an acuminate apex, while the outer perianth members terminate in an elongated mucro, which is probably equivalent to the "cornet" in the case of *Abolboda Poarchon* Seub., discussed in a preceding paragraph.

### Commelinaceae

The leaves of this family differ from most of those hitherto considered in their very complete differentiation. They usually



have a conspicuous sheath, sharply marked off from a limb, from which it may or may not be separated by a distinct petiolar region. Fig. 9 represents the leaf of *Streptolirion volubile* Edgw., in which all these parts are well developed. In *Commelina*, *Aneilema*, and *Tradescantia* there is a striking range of form in the limb, which in different species shows (within each genus) gradations from linear to ovate.

### Pontederiaceae

Fig. 8 A represents what is perhaps the most complex type of leaf met with in the Farinosae, that of *Eichhornia speciosa* Kth. (*Pontederia crassipes* Mart.). The ligular sheath (*lig. s*, fig. 8 A, B) with its lobed apex, almost suggesting a second leaf blade, to which attention has been drawn by GLÜCK (12), is, as he points out, unparalleled among monocotyledons; it may perhaps be remotely compared with the curious frill-like top of the ochrea of a *Polygonum* from Java, figured by VELENOVSKÝ (18, fig. 277). The petiole of *E. speciosa* is dilated, and terminates in a limb, which, as shown in a previous paper (1), possesses both normal and inverted bundles (fig. 8 C). In this paper it was recorded that inverted bundles occurred in the limb of *Eichhornia*, *Pontederia*, and *Heteranthera*. The family also contains three other genera, *Monochoria*, *Reussia*, and *Hydrothrix*. In *Monochoria plantaginea* Kth. I have now been able to observe that inverted as well as normal strands occur, and in a very small fragment of the leaf of *Reussia subovata* Solms, the only material available from this genus, I again found both types of strand. It has thus been possible to establish the occurrence of inverted strands in five genera of the Pontederiaceae; the sixth, *Hydrothrix*, is an aquatic plant in which it is useless to look for this anatomical peculiarity, since, as GOEBEL has shown, the leaf is so much reduced as to be traversed by one vascular strand alone (1).

The shape of the limb in the Pontederiaceae ranges from the narrow, almost linear form sometimes met with in *Monochoria plantaginea*, to broader types with a cordate base, such as *Pontederia nymphaefolia* Kth., or with an auricled base, such as that illustrated in *M. hastaefolia* Presl (fig. 7).



### Philydraceae

This small family consists of four species assigned to three genera. Sections were secured of three of these species, one belonging to each genus. The monotypic *Philydrum lanuginosum* Banks (fig. 22) has an ensiform leaf, whose shape and plan of vascular anatomy recall *Anarthria scabra* R.Br.; the leaf, however, is conspicuously lacunate. *Pritzelia pygmaea* F. Muell., representing the second of these monotypic genera, is related to *Philydrum* in its leaf structure, very much as *Anarthria gracilis* is related to *A. scabra*. The leaf of *Pritzelia* has a sheathing base (fig. 21 A) and a limb, which so closely approximates to radial structure that it is not possible to determine from internal evidence which is the median bundle (fig. 21 B). The leaf contains a number of large, solitary, acicular crystals (*c*, fig. 21 C). The leaves of the third genus, *Helmholtzia*, have been described as equitant and ensiform, but Dr. STAPF has been so kind as to inform me that in both the two species of which the genus consists, *H. acorifolia* F. Muell. and *H. glaberrimum* Hook. f., the vaginal portion of the leaf is strongly keeled, and that this keel runs as a midrib throughout the "vertical" limb. The limb is thus expanded in a plane at right angles to the truly ensiform limb of *Philydrum*. In accordance with this difference of construction, the leaf anatomy of the species which I have been able to examine, *H. acorifolia*, proves to be dorsiventral, with palisade parenchyma on the adaxial surface (fig. 23 A, B). The most striking feature of the leaf from the present standpoint is that, despite its dorsiventrality, it is characteristically phyllodic in structure, containing, besides normally orientated bundles (*nb*), others that are inverted (*ib*). Fig. 23 C shows the inverted group from the upper side of the midrib, in greater detail.

### Conclusions

#### CLASSIFICATION OF LEAF TYPES IN FARINOSAE

In the preceding pages the treatment of the leaves of this cohort has been almost exclusively descriptive, but I propose now to consider the interpretation of their morphology. The most



concise way is probably by means of a classification, based on the phyllode theory, of the principal types of leaf enumerated in dealing with the various families. On this basis the leaves of the Farinosae fall into the following six groups:

1. Phyllodes consisting of a sheathing base, and an ensiform limb equivalent to a petiole flattened in the vertical plane; for example, *Anarthria scabra* R.Br. (Restionaceae), fig. 3; *Xyris* (many species) (Xyridaceae), figs. 12, 14, 18; *Philydrum* (Philydraceae), fig. 22.

2. Phyllodes consisting of a sheathing base, and a limb departing little in character from a normal petiole and containing an arc or ring of bundles; for example, *Anarthria gracilis* R.Br. (Restionaceae), fig. 4; *Elegia deusta* Kth. (Restionaceae) (10, fig. 5 A, B); *Gaimardia australis* Gaudich. (Centrolepidaceae), fig. 5; *Xyris teretifolia* Pouls. (Xyridaceae) (16, fig. 3); *Pritzelia pygmaea* F. Muell. (Philydraceae), fig. 21.

3. Phyllodes essentially similar to (2), but in which the petiolar limb is reduced to a mere point; for example, *Leptocarpus peronatus* Mast. (Restionaceae), fig. 2; *Eriocaulon cuspidatum* Dalz (Eriocaulaceae), fig. 19; some Bromeliaceae.

4. Phyllodes similar to (3), but further reduced until they consist of leaf bases alone; for example, many Eriocaulaceae and Bromeliaceae.

5. Phyllodes in which the whole or the distal region of the petiole is flattened in the horizontal plane into a pseudolamina, containing inverted as well as normal bundles; for example, Pontederiaceae (figs. 7, 8); *Helmholtzia acorifolia* F. Muell. (Philydraceae), fig. 23.

6. Phyllodes in which the whole or the distal region of the petiole is expanded in the horizontal plane to form a pseudolamina without inverted bundles; for example, many Commelinaceae; *Rapatea* (Rapateaceae), figs. 24, 25.

#### COMPARISON WITH LEAVES OF OTHER COHORTS

One of the most striking results elicited by a general study of monocotyledonous leaves is the way in which certain leaf types recur again and again in this group, among plants by no means closely allied to one another. The leaves of the Farinosae afford many examples of these parallelisms. I will confine myself to an attempt to trace some of the relations between the leaf types of



the Farinosae and those of two other cohorts, Helobieae and Liliiflorae; the Liliiflorae include those monocotyledons most nearly related to the Farinosae (11), while the Helobieae are somewhat more remote.

The ribbon leaves of certain aquatic species of *Eriocaulon* recall the leaves of a corresponding form met with so frequently among the Helobieae (7), although, if my interpretation be correct, the ribbon leaves of Helobieae are of petiolar nature, while in those of *Eriocaulon* merely the leaf base is represented. Although the proportion of the parts is so different, it is such a leaf as that of *Restio tremulus* (fig. 1A), rather than that of a submerged *Eriocaulon*, which is equivalent to the ribbon leaf of, for instance, *Cymodocea nodosa* of the Potamogetonaceae (7). On the other hand, those leaves of the Farinosae in which the limb, although linear, is rather awl-like than ribbon-like, such as *Tillandsia usneoides* (Bromeliaceae, fig. 20), and *Gaimardia australis* (Centrolepidaceae, fig. 5), may be closely compared with *Cymodocea manatorum* (7). The venation of the limb of *Streptolirion volubile* of the Commelinaceae again (fig. 9) resembles that of *Alisma parnassifolium* (7). A contrast with the Helobieae, however, is furnished by *Monochoria hastaeifolia* (fig. 7), whose venation is essentially different from those of the species of *Sagittaria*, which it recalls in the outline of its pseudolamina (7). Turning to more detailed structure, the inverted bundles in the leaf limb of the Pontederiaceae and of *Helmholtzia* find their analogue in those of certain Hydrocharitaceae.

The occurrence of the ensiform leaf in the Farinosae, both in the Restionaceae, Xyridaceae, and Philydraceae, is another instance of the widespread distribution of this leaf type among the monocotyledons. It is known from the Helobieae, Spathiflorae, Liliiflorae, and Microspermae, as well as in the Farinosae. Not only in form, but also in internal structure, this type of leaf shows remarkable uniformity in the different groups. *Xyris Wallichii* (fig. 12A) and *X. brevifolia* (fig. 18A), with their alternating bundles, can be paralleled in *Iris* (1, 6). The fibrous margins, also, which are so marked a feature of the ensiform leaves of many Liliiflorae (6), reappear in *Xyris*. For comparison with the leaves



of the Farinosae, fig. 6 *A* and *B* show a section of the ensiform limb of *Hewardia tasmanica* Hook. (Liliaceae). It will be seen that in the distribution of the marginal fibers it resembles both *Tritonia* (fig. 10), and *Xyris Wallichii* (fig. 12 *C*) and *X. anceps* (fig. 14 *D*). This similarity is also carried into the details of the vascular system. Fig. 6 *A* shows examples from the limb of *Hewardia* of opposite bundles imbedded in a common fibrous sheath, and thus resembling the pair of bundles from the limb of *Xyris montivaga* Kth., shown in fig. 15. With this may also be compared the paired bundles of *Tofieldia* of the Liliaceae (1), *Tetroncium* of the Juncaginaceae (7), and *Tritonia* (fig. 16 *A, B*) and *Moraea Robinsoniana* (6). These bundle pairs are not only characteristic of the ensiform leaves of monocotyledons, but may be found also among the *Acacia* phyllodes, with which I believe these leaves to be homologous; they occur, for instance, in *Acacia neurophylla* (6). In addition to these bundle pairs, which clearly originate by more or less complete fusion of strands belonging to the opposite sides of the phyllode, *Xyris* also shows bundle groups of a different nature, illustrated here in the case of *Xyris asperata* (fig. 13 *A-C*) and *X. anceps* (fig. 14 *A*). These find their parallel in the tribe Johnsonieae of the Liliaceae (5). In the limb of *Arnocrinum Drummondii* Endl. there are bundle groups imbedded in fibers, which may be compared with those of *Xyris asperata*. It is true that they do not, as in the case of *Xyris*, occur in an ensiform leaf, but the ensiform leaf type is found in *Johnsonia*, to which *Arnocrinum* is probably more nearly related than it is to the five other members of the tribe.

The Farinosae furnish additional evidence for the close relationship of the ensiform and "radial" types of leaf. This relation, to which attention has already been called, both in the case of the leaves of the Liliiflorae and of the phyllodes of *Acacia*, is displayed with special clearness in *Iris*, among whose species there are examples of both forms of leaf, and also of intermediate types. In the Restionaceae, Xyridaceae, and Philydraceae there are comparable cases. Within the genus *Anarthria* both types are found (cf. figs. 3 and 4), and the same is true of *Xyris* (cf. figs. 12, 14, 18 with POULSEN'S fig. 3 of *X. teretifolia*, 16); while the ensiform



leaf of *Philydrum* (fig. 22) may be compared with the "radial" leaf of the related genus *Pritzelia* (fig. 21).

The type of leaf consisting of a sheathing leaf base terminating in a more or less cylindrical apex, which I interpret as a reduced petiole, occurs both in the Farinosae and Liliiflorae. For instance, the leaf of *Elegia deusta* Kth. (Restionaceae) is closely similar to that of *Distichia clandestina* Buch. of the Juncaceae (10). The apical tendril of *Flagellaria* (Flagellariaceae) also recalls that of *Gloriosa* and other Liliaceae. I hope to discuss the morphology of these leaf tendrils in a later paper.

To complete the parallel between the leaves of the Farinosae and those of the Liliiflorae, it may be noted that the limbs of the Pontederiaceae and of *Helmholtzia*, with their inverted bundles, to some extent approach those of certain species of *Allium* (5), and of such Amaryllids as *Zephyranthes* (8); while the similarity in shape of the cordate leaf limb of the Commelinaceous climber, *Streptolirion volubile* (fig. 9), and that of various Dioscoreaceae and Liliaceae is of wider interest, since it is an example of the recurrence of a form which appears again and again among monocotyledons. In former papers (1, 4) I have brought together a number of instances, from this class, of leaves with a cordate base; the list of families in which leaves of this type are found may now be increased to ten by the addition of the Stemonaceae, Amaryllidaceae, and Hydrocharitaceae. This comparison between the leaves of the Farinosae and those of the Helobieae and Liliiflorae emphasizes again the important part which parallelism of development has played in the evolution of the monocotyledonous leaf. The tendency for related stocks (even those whose affinity is far from close) to progress along corresponding lines is no doubt a very general feature of evolutionary history, although its prevalence is only gradually receiving full recognition. The fact that, in the monocotyledonous leaf, such parallelisms are displayed to an almost exaggerated degree, becomes to some extent explicable, if this organ is regarded as a phyllode consisting of leaf base and petiole alone. The loss of the lamina would inevitably impose restrictions upon the further evolution of the leaf, by confining its potentialities within a narrowed boundary. It might thus



induce a tendency to the repetition of a definite series of forms, monotonous in the basic features of their construction, but endlessly varied within their given limits.

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### LITERATURE CITED

1. ARBER, AGNES, The phyllode theory of the monocotyledonous leaf, with special reference to anatomical evidence. *Ann. Botany* 32:465-501. 1918.
2. ———, The vegetative morphology of *Pistia* and the Lemnaceae. *Proc. Roy. Soc. B.* 91:96-103. 1919.
3. ———, Leaf-base phyllodes among the Liliaceae. *BOT. GAZ.* 69:337-340. 1920.
4. ———, Tendrils of *Smilax*. *BOT. GAZ.* 69:438-442. *pl.* 22. 1920.
5. ———, On the leaf structure of certain Liliaceae, considered in relation to the phyllode theory. *Ann. Botany* 34:447-465. 1920.
6. ———, The leaf structure of the Iridaceae, considered in relation to the phyllode theory. *Ann. Botany* 35:301-336. 1921.
7. ———, Leaves of the Helobieae. *BOT. GAZ.* 72:31-38. *pl.* 1. 1921.
8. ———, Leaves of certain Amaryllids. *BOT. GAZ.* 72:102-105. 1921.
9. ———, On the development and morphology of the leaves of palms. *Proc. Roy. Soc. B.* 93:249-261. 1922.
10. ———, On the leaf-tips of certain monocotyledons. *Linn. Soc. Jour. Bot.* 46:467-476. 1922.
11. ENGLER, A., Die systematische Anordnung der monokotyledoneen Angiospermen. *Abhandl. Akad. Wiss. Berlin. Abhandl. II.* 1-55. 1892.
12. GLÜCK, H., Die Stipulargebilde der Monokotyledonen. *Verhandl. Nat.-Med. Vereins Heidelberg. N.F.* 7<sup>1</sup>:1-96. *pls.* 1-5. 1901.
13. GOEBEL, K., Organographie der Pflanzen. Zweite Auflage. Teil 1. *Allgemeine Organographie.* 1913.
14. MCLEAN, R. C., The utilization of herbarium material. *New Phytol.* 15:103-107. 1916.
15. MEZ, C., Bromeliaceae, in MARTIUS, C. F. P. VON, *Flora Brasiliensis* 3: part 3. 1892.
16. POULSEN, V. A., Anatomiske Studier over Xyris-Slaegtens vegetative Organe. *Videnskab. Meddel. Naturhist. Forening Kjøbenhavn.* pp. 133-152. *pls.* 2, 3. 1892 for 1891.
17. SEUBERT, M., Xyridaceae and Mayaceae, in MARTIUS, C. P. F. VON, *Flora Brasiliensis.* 3: part 1. 1855.
18. VELENOVSKÝ, J., Vergleichende Morphologie der Pflanzen. Teil 2. 1907.

### EXPLANATION OF PLATES I-III

Throughout, xylem (*xy*) shown in black; phloem (*ph*) in white; and fibers (*f*) dotted; *lac*, lacuna; *pp*, palisade parenchyma; *mb*, median bundle;



*ep*, epidermis; *s*, sheath; *pet*, petiole; *l*, limb; *n*, node; *ax*, axis; in all sections of equitant leaves, the identity of abaxial and adaxial margins has had to be decided on internal evidence, owing to fragmentary character of herbarium material available.

## PLATE I

FIG. 1 *A-D*.—*Restio tremulus* R.Br.: *A*, axis bearing leaf ( $\times \frac{1}{2}$ ); *B*, transverse section sheath of leaf ( $\times 14$ ); *C* and *D*, transverse section limb of another leaf ( $\times 23$ ); *D* nearer apex than *C*.

FIG. 2.—*Leptocarpus peronatus* Mast., axis bearing leaf ( $\times \frac{1}{2}$ ).

FIG. 3 *A, B*.—*Anarthria scabra* R.Br.: *A*, transverse section leaf limb ( $\times 14$ ), section slightly reconstructed at upper margin; *B*, dorsal (abaxial) margin of *A* ( $\times 77$ ).

FIG. 4 *A-C*.—*Anarthria gracilis* R.Br., transverse section one leaf: *A*, sheath (section slightly reconstructed at margins of sheath); *B*, basal part of limb; *C*, limb ( $\times 23$ ).

FIG. 5 *A-C*.—*Gaimardia australis* Gaudich.: *A*, leaf ( $\times 3\frac{1}{2}$  circa); *B* and *C* transverse section of one leaf ( $\times 77$ ); *B*, sheath; *C*, limb.

FIG. 6 *A, B*.—*Hewardia tasmanica* Hook. (for comparison): *A*, transverse section leaf limb ( $\times 23$ ); *B*, upper margin of *A* ( $\times 77$ ).

FIG. 7.—*Monochoria hastaefolia* Presl, limb of leaf to show venation ( $\times \frac{1}{2}$ ).

FIG. 8 *A-C*.—*Eichhornia speciosa* Kth.: *A*, small leaf to show dilated petiole and ligular sheath (*lig.s*) ( $\times \frac{1}{2}$ ); *B*, top of sheath from *A*, viewed from adaxial side to show three ligular lobes ( $\times \frac{1}{2}$ ); *C*, transverse section through margin of leaf limb in *A*, in direction of arrow ( $\times 14$ ); *nb*, normally orientated bundles; *ib*, inverted bundles.

FIG. 9.—*Streptolirion volubile* Edgw., axis bearing leaf ( $\times \frac{1}{2}$ ).

FIG. 10.—*Tritonia*, garden hybrid (for comparison), margin of ensiform leaf ( $\times 193$ ).

FIG. 11 *A-B*.—*Centrolepis aristata* R and S.: *A*, axis of small plant bearing inflorescence inclosed in bracts (*b, b*), foliage leaf to right ( $\times \frac{1}{2}$ ); *B*, transverse section sheath foliage leaf ( $\times 23$ ); *B*, transverse section limb ( $\times 77$ ); *bs*, bundle sheath, consisting of one inner thick-walled layer, and one outer layer of larger cells with thinner walls.

## PLATE II

FIG. 12 *A-C*.—*Xyris Wallichii* Kth.: *A*, transverse section leaf limb ( $\times 23$ ); *B*, stomate from *A* ( $\times 198$ ); *C*, margin of *A* ( $\times 198$ ).

FIG. 13 *A-C*.—*Xyris asperata* Kth. (*trachyphylla* Mart.): *A*, transverse section transition region between sheath and limb ( $\times 23$ ) to show bundle groups; *B*, bundle group marked *x* in *A* ( $\times 77$ ); group of four bundles (*b<sub>1</sub>, b<sub>2</sub>, b<sub>3</sub>, b<sub>4</sub>*), in common fibrous sheath, from transverse section of leaf limb ( $\times 318$ ).

FIG. 14 *A-D*.—*Xyris anceps* Lam.: *A*, transverse section limb of leaf ( $\times 23$ ); *b<sub>1</sub>*, single bundle; *b<sub>2</sub>*, group of two bundles; *b<sub>3</sub>*, group of three bundles; *B*, apex of leaf limb viewed as solid object ( $\times 23$ ); *C*, fibrous margin of leaf viewed as solid object ( $\times 77$ ); *D*, transverse section margin of *A* ( $\times 77$ ).



FIG. 15.—*Xyris montivaga* Kth.: pair of opposite bundles ( $xy_1$  and  $ph_1$ ,  $xy_2$  and  $ph_2$ ) in common fibrous sheath ( $\times 318$ ); similar to  $b_2$  in fig. 14 A (*X. anceps*).

FIG. 16 A, B.—*Tritonia* (garden hybrid) for comparison, lettering as in fig. 15; fibers represented in black (instead of white with double lines indicating thickness of walls, as in other figures): A, pair of opposite bundles from transverse section of leaf limb ( $\times 318$ ); B, similar pair of bundles, but with xylems fused ( $\times 318$ ).

FIG. 17 A-C.—*Xyris gracilis* R.Br.: A, leaf consisting mainly of leaf sheath, with reduced limb ( $l$ ); B, apex of another reduced leaf in which limb is absent (both natural size); C, transverse section of leaf shown in B (slightly enlarged).

FIG. 18 A-B.—*Xyris brevifolia* Mich.: A, transverse section leaf limb ( $\times 23$ ); B, marginal bundle such as that marked  $x$  in A ( $\times 193$ ).

FIG. 19 A-D.—*Eriocaulon*: A and B, *E. septangulare* With.; A, transverse section of limb of leaf ( $\times 23$ ); B, lamella marked  $x$  in A ( $\times 77$ );  $ue$ , upper epidermis,  $le$ , lower epidermis;  $d$ , fragment of diaphragm seen in surface view; C, *E. Wallichianum* Mart. f. *submersa*, apex of leaf ( $\times \frac{1}{2}$ ); D, *E. cuspidatum* Dalz., apex of leaf to show mucro ( $\times \frac{1}{2}$ ).

FIG. 20 A, B.—*Tillandsia usneoides* L., transverse section leaf ( $\times 23$ ): A, sheath; B, limb.

#### PLATE III

FIG. 21 A-C.—*Pritzelia pygmaea* F. Muell., transverse section leaf: A, sheath; B, limb ( $\times 23$ ); orientation of B uncertain; C, margin of sheath in A ( $\times 77$ ) to show stomate ( $st$ ) and crystals ( $c$ ).

FIG. 22.—*Philydrum lanuginosum* Banks, transverse section limb of leaf ( $\times 14$ ).

FIG. 23 A-C.—*Helmholtzia acorifolia* F. Muell., A and B, transverse section limb of leaf ( $\times 23$ ): A, midrib region ( $mr$ ); B, margin, to show normally orientated bundles and bundle groups ( $nb$ ) and inversely orientated bundles and bundle groups ( $ib$ ); C, inverted bundles of midrib from section similar to A ( $\times 77$ ).

FIG. 24.—*Rapatea longipes* Spr., small leaf ( $\times \frac{1}{2}$ ).

FIG. 25 A-C.—*Rapatea angustifolia* Spr.: A and B, transverse section leaf ( $\times 14$ ); A, sheath; B, limb; C, median bundle ( $mb$ ), of limb in B ( $\times 77$ ).

FIG. 26 A-C.—*Cephalostemon affinis* Koern: A, B, transverse section leaf ( $\times 14$ ); A, sheath; B, limb; C, median bundle of limb ( $\times 77$ ).

FIG. 27 A-B.—*Mayaca fluviatilis* Aubl.: A, leaf ( $\times \frac{1}{2}$ ); B, leaf apex ( $\times 14$ );  $vb$ , vascular strand.